Topical review

Non-photochemical chlorophyll fluorescence quenching: mechanism and effectiveness in protection against photodamage

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One-sentence summary: A review of the current state of the knowledge of the mechanism and protective effectiveness of non-photochemical chlorophyll fluorescence quenching is presented.

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Abstract

The mechanism of non-photochemical chlorophyll fluorescence quenching, NPQ, and its role in protecting plants against photoinhibition is reviewed. An introduction to the phenomenon, a brief history of the major milestones, definitions, and a discussion of quantitative measurements of NPQ have been presented. The up-to-date knowledge and unknown aspects in the NPQ scenario that includes proton gradient (ΔpH) – *trigger*, the photosystem II (PSII) light harvesting antenna (LHCII) – *site*; changes in the antenna induced by ΔpH – *change* leading to creation of the *quencher* have been discussed. It is concluded that the minimum requirement for NPQ *in vivo* consists of ΔpH, LHCII complexes and the PsbS protein. The most important unknown in the NPQ scenario is highlighted to be the mechanism of PsbS action upon the LHCII antenna. A novel emerging technology for the assessment of the photoprotective 'power' of NPQ has been reviewed and its insightful outcomes are explained using several examples.

"Real knowledge is to know the extent of one's ignorance."

Confucius

Non-photochemical chlorophyll fluorescence quenching (NPQ) refers to a process of increased absorbed light energy dissipation into heat that takes place in the photosynthetic membrane of plants, algae and cyanobacteria (Demmig-Adams et al., 2014). Early photosynthetic organisms facing the problem of shady environments evolved the light harvesting antenna that collect the dilute energy of light for the photosynthetic reaction centres (Clayton, 1980; Blankenship, 2002). However, high light exposure in this case causes rapid saturation of the photosynthetic reaction centres and their eventual closure, leading to a reduction in the fraction of energy utilized in photosynthesis and the subsequent build-up of harmful excess excitation energy in the photosynthetic membrane (Björkman and Demmig-Adams, 1995). This energy can damage the most delicate part of the photosynthetic apparatus, the photosystem II (PSII) reaction centre (RCII) that drives water splitting and oxygen evolution (Powles, 1984; Barber, 1995; Ohad et al., 1984). A RCII repair mechanism does exists but the process occurs on the time scale of hours (Barber and Andersson, 1992; Aro et al., 1993; Nixon et al., 2010; Nath et al., 2013). In addition, excess light can potentially be harmful to the antenna pigments (Fleming et al., 2012). This can lead to a sustained decline in photosynthetic efficiency and in extremes to the death of the photosynthetic cell, tissue or organism.

Evolution supplied a range of solutions to the problem of high light exposure that vary in efficiency, level of action and promptness of response (Gall et al., 2011; Niyogi and Truong, 2013; Ruban, 2014; Demmig-Adams et al., 2014; Goss and Lepetit, 2015). There are adaptations to control light absorption capacity as well as adaptations that deal with the light energy that has already been captured (Chow et al., 1988; Koller, 1990; Ruban, 2009; Cazzaniga et al., 2013; Xu et al., 2015). At the molecular level there is both long-term (acclimation) and short-term (regulatory mechanisms) control of the input of light energy into RCs. The first type is predominantly developmental in nature, and is the result of light-dependent regulation of complex gene expression, occurring on transcriptional, translational and post-translational levels (Anderson et al., 1988). However, since the response time of acclimation is long, it limits photoprotective efficiency while at the same time consuming energy and resources. On its own it is insufficient since profound damage to the RCII can occur within minutes of excess light exposure (Tyystjarvi and Aro, 1996).

NPQ is a molecular adaptation that represents the fastest response of the photosynthetic membrane to the excess light (Demmig-Adams et al., 2014). The NPQ process directly or indirectly relates to the processes of light harvesting by the photosynthetic antenna complexes,

their structure, captured energy transfer to reaction centers, electron transport, proton translocation across the membrane, ATPase activity and carbon assimilation (Walker, 1987; Ruban, 2013; Demmig-Adams et al., 2014). At various times NPQ research progressed through new developments in the fields of defining and quantifying this protective process (Papageorgiu and Govindjee, 1968; Murata and Shugahara, 1969; Schreiber, 1986; Oxborough and Horton, 1988; Weis and Berry, 1987), the structure of the photosynthetic antenna complexes (Nield and Barber, 2006; Liu et al., 2004) and their organisation in the membrane (Dekker and Boekema, 2005; Ruban and Johnson, 2015), dynamics of the antenna complexes (Garab et al., 1988; Ruban et al., 1994; Miloslavina et al., 2008; Krüger et al., 2012, Liguori et al., 2015) pigment compositions (Rees et al., 1989; Demmig-Adams, 1990) and dynamics in the membrane (Demmig-Adams and Adams III, 1992; Matsubara et al., 2001; Jahns et al., 2009), excitation energy transfer and dissipation (van Amerongen et al., 2000; Polivka and Sundstrom, 2004; Renger and Holzwarth, 2008; Cheng and Fleming, 2009; Scholes et al., 2011). It was a long and often convoluted path towards the complete understanding of the molecular mechanism. Indeed, it took some time to define and separate NPQ, to learn how to measure and quantify it, to obtain molecular insights into antenna structure, to learn its dynamic nature and understand its role in protection. Recent years witnessed a great emergence of review articles on various aspects of NPQ. A recent collection of which have been published in the 40th volume of the series Advances in Photosynthesis and Respiration 2014 (Demmig-Adams et al., 2014). Hence, the aim of this review is to provide a complementary information highlighting the most recent known and unknown aspects of the most investigated *mechanism* of NPQ that takes place in plants. This article also discusses emerging work on quantitative approaches to assessing the *effectiveness* of NPQ in protection against photoinhibition.

DEFINITION OF NPQ

NPQ was introduced as a reflection of the processes that arise in the photosynthetic membrane that are not photochemical in origin. Indeed, the activity of the RCII causes a significant decrease, or quenching, of chlorophyll fluorescence, since it consumes light energy that otherwise could be released through fluorescence, interconversion or intersystem crossing (Duysens and Sweers, 1963; Govindjee and Papageorgiu, 1971; Myers, 1974). However, it was also discovered that fluorescence can be quenched in conditions when all RCII are closed, hence not consuming any absorbed light energy (Papageorgiu and Govindjee, 1968; Murata and Shugahara, 1969; Wright and Crofts, 1970). This was achieved first by using the PSII acceptor site inhibitor DCMU added to chloroplasts constantly illuminated by actinic light. The inhibitor caused the closure of RCII's within the first second of illumination, quickly reversing the

photochemically quenched fluorescence while the remaining part of the quenched fluorescence reversed on a much slower time scale (Papageorgiu and Govindjee, 1968). This slowly relaxing quenching was called 'non-photochemical quenching', or energy-dependent quenching qE (Wright and Crofts, 1970). The term qE still remains popular and is considered to be the major part of NPQ (Figure 1A).

In the 1980's the introduction of the pulse amplitude modulated (PAM) fluorescence technique opened up a powerful opportunity for the detailed study of NPQ (Shereiber, 1986; Oxborough and Horton, 1988). Figure 1A depicts a typical PAM induction measurement assessing the state of PSII in the dark, the F_o fluorescence level, when all RCIIs are open and the F_m level, when all of them are closed by the high intensity pulse (normally of 0.5-1.0 s duration). From this simple start one can calculate the quantum efficiency of PSII as $\Phi_{PSII} = (F_m-F_o)/F_m$. In fact this is actually the relative amount of fluorescence that was photochemically quenched due to the activity of the reaction centres. It is interesting to note that the fluorescence does not immediately return to the initial F_o level which is due to the fact that the acceptor site of the PSII stays reduced for some time. This can be accelerated by the use of far red light that preferentially excites photosystem I (PSI), causing faster oxidation of the Cyt*b*/*f* complex and the pool of mobile electron carriers, plastoquinones (PQ), that removes electrons from PSII (Hill and Bendall, 1960; Blankenship, 2002). Then the actinic light illumination was applied for about 5 min. During this time saturating light pulses are used every minute to determine the level of F_m. It can be clearly seen that this level is being progressively quenched and stabilises at the end of the illumination period. The quenched F_m is termed F_m'. Hence the level of NPQ can be calculated as $(F_m-F_m')/F_m'$. Another parameter called qN is used to calculate non-photochemical quenching: $qN = (F_m-F_m')/F_m$. This effectively gives a percentage of quenching in a similar manner to Φ_{PSII}. The NPQ calculation reflects the ratio of the rate constant of NPQ to the sum of the rest of the constants reflecting all other dissipation pathways in the membrane, such as fluorescence, internal and interconversion (Krasuse and Weis, 1991). qE is defined in the context of this analysis as the rapidly-reversing component of qN or NPQ (Figure 1A). Normally this component is considered to recover within 5 minutes of switching off the actinic light. It is worth noting that the trigger of qE, ΔpH, usually collapses within 10-20 s (Ruban, 2013). Hence, it was proposed in the early days of NPQ research that the process involved some conformational changes within the photosynthetic membrane that respond to ΔpH. As shown on the figure, qE appears to be the major component of NPQ. The rest used to be termed qI or the irreversible NPQ component related to photoinhibition/damage to RCII (Krause and Weis, 1991). Later, it was discovered that the formation of zeaxanthin is closely related to the NPQ mechanism (Demmig-Adams et al., 1989; Demmig-Adams, 1990; Demmig-Adams and Adams III, 1992; for review see Demmig-Adams et al., 2014) and as such a part of qI

is often termed qZ to reflect the long-term quenching effect that correlated with the presence of this pigment (Nilkens, 2010). In addition, other sustained components of NPQ have been reported that were triggered by low temperature acclimation (Verhoeven, 2013), prolonged illumination in the presence of zeaxanthin (Ruban and Horton, 1995), slow proton equilibration between different membrane compartments (Ruban and Horton, 1995; Joliot and Finazzi, 2010) or simply by formation of large levels of NPQ in some types of photosynthetic material (Ruban et al., 1993; Ruban et al., 2004; Ware et al., 2015). Hence qI appeared to be a very complex component of NPQ that remained difficult to interpret and the temporal criterion for quantification of qE is rather ambiguous. Hence, we will use here the term protective NPQ (or just NPQ) instead of qE, meaning that the former includes all moderately or slowly reversible components that are not related to photoinhibition (see for details in PROTECTIVE EFFECTIVENESS OF NPQ).

MECHANISM OF NPQ

NPQ resides in the antenna (Bassi and Caffarri, 2000; Fleming et al., 2012; Ruban et al., 2012; Wilk et al., 2013) (*site*) that undergoes a *change* triggered by ΔpH (*trigger*) (Horton et al., 1996; Strand and Kramer, 2014). As a result of this change the *quencher* pigment(s) start receiving and dissipating the energy harvested by the LHCII antenna into heat. Hence ΔpH provides a feed-back control over light harvesting efficiency in the photosynthetic membrane (Ruban et al., 2012; Strand and Kramer, 2014).

Trigger: protons

NPQ is triggered by ΔpH either directly by protonation of antenna components or indirectly by the xanthophyll cycle(s) activity (Ruban et al., 2012). It also makes sense to refer to the proton gradient as the *trigger* since in some organisms like diatom algae where large levels of NPQ can be induced and sustained in the dark or upon addition of uncouplers in the absence of ΔpH (Ruban et al., 2004; Lepetit et al., 2012). It was also established that acidification of the incubation buffer can induce fluorescence quenching that possessed features similar to NPQ (Rees et al., 1992). This finding provided a justification of the use of acidification technique in studies of fluorescence quenching in isolated antenna complexes (Ruban et al., 1994; Bassi and Caffarri, 2000). Importantly, since ΔpH build-up is generated as a result of electron transport, a variety of pathways contribute to its amplitude and the reader is referred to the most recent comprehensive review (Strand and Kramer, 2014). In addition, ATPase by consuming protons exerts a modulatory effect upon ΔpH. Also, a recent report showed that not only ATPase but a specialised proton/potassium antiporter can influence the rate of NPQ relaxation at low light by accelerating the collapse of ΔpH (Armbruster et al., 2014). In fact, the *trigger* is kept under control too (Figure

1B, regulatory points 1&2). It appears that cyclic electron transport around PSI is the major contributor to the component of ΔpH that triggers the larger part of NPQ (Munekage et al., 2004). Recent work by Sato and co-workers (2015) discovered that the cyclic electron transport-generated ΔpH contributes 60-80% to NPQ formation. Therefore, the ratio between PSII and PSI defined, for example, in the course of acclimation is likely to affect the *trigger* and therefore the amplitude of NPQ (Brestic et al., 2015). Remarkably, chloroplasts from plants grown on lincomycin, and have therefore lost almost all of PSII and 80% of PSI, were found to form levels of ΔpH close to those from the control plants as well as to form very large levels of NPQ (Belgio et al., 2012; Belgio et al., 2015). The modulation of ΔpH by artificial proton shuttles such as diaminodurene (DAD) has recently been successfully used to provide vital mechanistic clues about the sensitivity of responses of antenna components to lumen acidification during the induction of NPQ (see below in *Site*: LHCII antenna and PsbS). Lumen protons target three key components involved in NPQ: violaxanthin de-epoxidase (Figure 1B, target point 3) (Jahns et al., 2009), the PsbS protein (Figure 1B, target point 4) (Li et al., 2004) and the LHCII antenna (Figure 1B, target point 5) (Ruban et al., 1994; Walters et al., 1994; Ruban et al., 1996; Liu et al., 2008; Belgio et al., 2013). The pK of the lumen-exposed side of the thylakoid membrane is as low as 4.1 (Åkerlund et al., 1979). The estimates of the *in vivo* lumen acidification as a result of ΔpH formation give pH 5.5 (Noctor et al., 1991; Kramer et al., 1999). The pK for NPQ in chloroplasts devoid of zeaxanthin is 4.7 and pK of the quenching in the isolated major LHCII complex without zeaxanthin is about 4.5 (Wentworth et al., 2001) but is 1-2 units of pH higher in the presence of zeaxanthin or in monomeric LHCII, CP26 (Ruban and Horton, 1999; Wentworth et al., 2001). The pK for PsbS according to the study by Dominici and co-workers (2002) should be in the region of 6.0-6.5. A similar pK for the violaxanthin de-epoxidation was reported by Jahns and co-workers (2009). Hence, it appears that the most lumen pH sensitive components of the thylakoid membrane are PsbS, violaxanthin de-epoxidaze, monomeric antenna complexes and LHCII that bind zeaxanthin produced by de-epoxidase (Ruban at al., 2012). Therefore, for the LHCII antenna to respond to lumen pH (Figure 1B, target point 5) and become quenched it is important to achieve activation of de-epoxidase (target point 3) in order to produce zeaxanthin and activation of the PsbS protein (target point 4). Both LHCII and PsbS contain a number of lumen exposed residues that can receive protons. Two of them have been identified for monomeric LHCII and two for PsbS using DCCD labelling and site-directed mutagenesis (Walters et al., 1996; Li et al., 2004). However, tritium labelling of LHCII *in vivo* suggested that each monomer can sequester up to 17 protons (Zolotareva et al., 1999). It may well be possible that since monomeric antenna receive protons at lower levels of ΔpH they are the primary sites for the quenching that eventually spreads into the bulk of LHCII trimers. The idea that the minor antenna are the site for NPQ is currently

being the most supported by the work of groups of Fleming and Bassi (Ahn et al., 2008; Avenson et al., 2009).

There was never an easy way to measure the proton gradient. The use of 9-aminoacridine was a most common way to assess it in thylakoids or chloroplasts (Ruban, 2013). However, it appears not to be an easy task to do this on leaves and the only method was the indirect measurement using the light-induced absorption change at 518 nm that is believed to reflect the electrochromic shift of carotenoids (Kramer et al., 1999). However, this method was recently subjected to a critical reassessment that claimed that the observed steady-state component of the 518 nm absorption change that was used as a measure of the proton gradient (Kramer et al., 1999) was due to the interference with the NPQ-associated absorption at 535 nm (for more detailed discussion see Johnson and Ruban, 2013). This work has also cast doubt that the electric field gradient $\Delta\psi$ makes a noticeable contribution to the proton motive force in photosynthesis. The 535 nm change is tightly related to NPQ and, since the latter is triggered by ΔpH, measurements of absorption at 518 nm would reflect to a certain extent the amplitude of NPQ and therefore, indirectly, ΔpH. Therefore development of accurate, direct and non-destructive ways to measure ΔpH *in vivo* would be a crucial step towards monitoring the dynamics of this important parameter in a course of light and metabolic alterations in order to find the causes of altered NPQ levels.

***Site*: LHCII antenna and PsbS**

Some 25 years ago modelling of the relationship between NPQ and the PSII yield prompted a point towards the involvement of the PSII antenna in NPQ (Genty et al., 1989). Indeed, the NPQ quencher was found to decrease not only F_m but F_o fluorescence (see Figure 1A) (Horton and Ruban, 1993). The quencher persisted at 77K and preferentially quenched major LHCII complex bands at 680 and 700 nm (Ruban et al., 1991). Early fluorescence lifetime analysis was consistent with quenching taking place in the PSII antenna (Genty et al., 1992). Later this type of spectroscopy revealed similarities between decay-associated spectral changes upon the transition into the quenching state in both isolated LHCII complexes and intact chloroplasts (Johnson and Ruban, 2009). Plants lacking a majority of LHCII antenna complexes displayed strongly reduced NPQ (Jahns and Krause, 1994; Havaux et al., 2007). The remaining quenching in the chlorina mutants or intermittent light grown plants was attributed to the presence of some minor LHCII antenna complexes (Jahns and Krause, 1994; Havaux et al., 2007) as was previously proposed (Andrews et al., 1995). NPQ was also found to be modulated by cross-linkers, tertiary amines, antimycin A, DCCD and magnesium in the same way as the quenching in isolated LHCII antenna complexes (Ruban et al., 1994; Ruban et al., 1996; Ruban et al., 1992; Johnson and Ruban, 2009). The latter was induced at the detergent concentration below *cmc* and led to the

aggregation of the complex. Hence, the hypothesis of the *in vivo* aggregation of the LHCII antenna as a mechanism underlying NPQ has been put forward (Horton et al., 1991) (for discussion see *Change*: LHCII aggregation and other). Moreover, discovery that the xanthophyll cycle carotenoids were localised exclusively in LHCII antenna complexes (Thayer and Thornber, 1992; Bassi et al., 1993) and later that NPQ was entirely dependent upon the xanthophylls zeaxanthin and lutein (Pogson et al., 1998; Niyogi et al., 2001) caused little doubt that the NPQ site was the LHCII antenna (for more details read Ruban et al., 2012).

The evolving knowledge of PSII antenna composition, structure and organisation in the photosynthetic membrane revealed its structural and functional heterogeneity (Boekema et al., 1995; Jansson, 1994; Dekker and Boekema, 2005; Caffarri et al., 2009; Kouřil et al., 2011; Kouřil et al., 2013). The current structure proposes that the LHCII antenna is built of three monomeric LHCII antenna complexes, CP24, CP26 and CP29, collectively called the minor LHCII antenna and several trimeric LHCII known as the major LHCII antenna. The minor LHCII antenna build the structural and apparently functional (Dall'Osto et al., 2014) bridge between the major trimeric LHCII complexes and the core antenna in the PSII supercomplex dimer (Figure 2). Three types of LHCII trimers are distinguished based on their binding strength to the PSII supercomplex: S, M and L, strongly, medium and loosely bound, respectively. Only the localisation of S and M trimers have been identified. It is supposed that loosely bound trimers are relatively free to diffuse in the membrane, therefore it is difficult to predict their localisation. There can be 2 to 4 and sometimes more loosely bound trimeric LHCII complexes per one PSII monomer (Melis and Anderson, 1983; Kouřil et al., 2012; Wientjes et al., 2013). Work on DCCD binding, *in vitro* quenching and carotenoid binding work on the monomeric LHCII complexes CP26 and CP29 showed that they are both capable acceptors of protons as well as able to attain large levels of quenching and are enriched in xanthophyll cycle carotenoids (Walters et al., 1994; Walters et al., 1996; Ruban et al., 1996; Ruban et al., 1997; Bassi and Caffarri, 2000). It allowed researchers to put forward a proposal that the site of NPQ is localized in the monomeric LHCII complexes (Bassi and Caffarri, 2000; Ahn et al., 2008; Avenson et al., 2009). This opinion was weakened by the fact that antisense and knockout mutants of *Arabidopsis* lacking one or even two of the three monomeric LHCII (CP24/29 double mutant) possessed significant levels of NPQ (Andersson et al., 2001; de Bianchi et al., 2008). In addition, the efficiency of violaxanthin de-epoxidation located in the L2 site (Pan et al., 2011) was found to be very low in the minor antenna complexes, particularly in CP29, due to a strong binding into the site (Duffy and Ruban, 2012) implying that they cannot bind any significant amounts of the postulated quencher zeaxanthin in this site. However, it may well be that the quenching in the monomeric LHCII antenna complexes proceeds by the same mechanism (Mozzo et al., 2008) as that suggested for the major trimeric LHCII (Ruban et al.,

2007). Now, further clarification of the role of monomeric LHCII complexes in NPQ is expected to come from a study of the already reported triple minor antenna knock-out mutant (NOM) (Dall'Osto et al., 2014).

Another component that was discovered to play a crucial role in enabling the rapidly-reversible component of NPQ, qE, is the PsbS protein (Li et al., 2000). Structural work on the localisation of this protein in the photosynthetic membrane suggested that it is not a part of the PSII supercomplex (Nield et al., 2000). Biochemical work convincingly showed that PsbS does not specifically bind pigments (Bonente et al., 2008). Recently the atomic structure of PsbS has been solved (Fan et al., 2015). The structure of the protein is a dimer that is more stable at low pH. Acidification was suggested to cause a conformational change associated with alteration in lumenal intermolecular interactions. Hence, it appears that PsbS acts rather like a *switch* that is triggered by ΔpH and not a quenching site. Therefore, this switch has to be localised closer to the LHCII antenna in order to prompt it into the NPQ state or make it sensitive to protonation (Ruban et al., 2012). It seems to be appropriate to use the term "sensitive" here since it was shown that qE can actually form without PsbS provided ΔpH is high enough (Johnson and Ruban, 2011). Hence, the model in Figure 1B draws a straight line from the *trigger* to *site* (LHCII antenna) (action point 5) bypassing PsbS and zeaxanthin and putting them rather as components of modulation. These components are actually important for physiological adjustment of NPQ (see in *Change*: LHCII aggregation and other). Since PsbS was not found in the PSII supercomplex it has got to be localised somewhere in the domains of the LHCII antenna (Figure 2). The recent report that biochemically probed the site of PsbS binding in PSII in the moss *Physcomitrella patens* proposed that in the dark the protein binds to several Lhcb proteins with preferential binding to the periphery of the LHCII M trimer of the PSII supercomplex (Gerotto et al., 2015). Hence this work has pointed out that the likely NPQ site is trimeric rather than monomeric LHCII complexes. However, it would be interesting to apply this approach to the higher plant PSII in both dark-adapted and NPQ states. Interestingly, plants that grew on lincomycin (mentioned above) and possessed very few RCII retaining trimeric and some reduced amounts of monomeric LHCII complexes, also contained PsbS protein (see above) (Belgio et al., 2012; Belgio et al., 2015). NPQ in these plants was modulated by PsbS (Ware et al., 2015) suggesting that the site of NPQ is LHCII antenna and PsbS together. However, this work did not prove that the monomeric LHCII was not involved, but it produced a simpler model system for NPQ studies. It looks like only ΔpH, the LHCII antenna and PsbS are required for NPQ *in vivo*. It is likely that PsbS is needed to make the LHCII antenna more rapidly responsive to natural levels of ΔpH. The structural arrangement of the LHCII antenna and PsbS around PSII does not seem to matter for the quenching to be observed, provided they are in the membrane. However, the core complex may play a role in

tuning NPQ kinetically by initiating the reassembly of the antenna around it in the dark (Dong et al., 2015; Ware et al., 2015). The notion that the RCII core complex is not essential for quenching is consistent with a recent work on reconstitution of PsbS and the major LHCII complex into liposomes (Wilk et al., 2013). Interestingly the liposomal system did not contain any minor antenna complexes suggesting that LHCII trimers are sufficient partners for PsbS interaction and formation of the *quencher*.

Change: LHCII rearrangements/aggregation and formation of the NPQ _quencher_

The requirement for the change in the LHCII antenna triggered by ΔpH was first proposed by the work of Horton's group (Horton et al., 1991). This was the hypothesis that stated that the proton gradient triggered LHCII antenna aggregation that was required to establish the NPQ state. Indeed, isolated major LHCII complex was shown to aggregate at low detergent concentration that was greatly enhanced by acidification of the incubation buffer and this process was followed by a fluorescence quenching that was strong enough to explain any levels of NPQ observed in nature (Ruban et al., 1994). Another attractive physiological implication of this hypothesis was that LHCII antenna aggregation was modulated by xanthophyll cycle carotenoids the fact that explained NPQ with and without zeaxanthin as well as the concept of 'plant illumination memory' and the effect of *hysteresis* (Horton et al., 1996; Ruban et al., 2012). Xanthophyll cycle carotenoids have been discovered to be localised in peripheral binding site V1 of the major LHCII complex (Ruban et al., 1999; Liu et al., 2004) and it is not excluded that they are also bound peripherally to the minor antenna complexes (Ruban et al., 1999; Xu et al., 2015). This peripheral localisation and ability to regulate LHCII antenna aggregation has been explained by different hydrophobicity/polarity of violaxanthin and zeaxanthin (Ruban and Johnson, 2010; Ruban et al., 2012). Presence of zeaxanthin was suggested to slow down reversibility of NPQ and promote the sustained component qZ due to the tuning of LHCII antenna into aggregation that is slowly-reversible (Noctor et al., 1991; Ruban and Horton, 1999). In addition, violaxanthin de-epoxidation was reported to alter LHCII antenna aggregation state *in vivo* as well as energy transfer pathways within LHCII antenna bringing minor LHCII antenna complexes such as CP29 to a closer contact with LHCII trimers (Ilioaia et al., 2013).

Although the LHCII antenna aggregation hypothesis for NPQ prompted much of research around LHCII complexes and many attempts to link it to NPQ using indirect biochemical and spectroscopic methods (for the recent review see Ruban et al., 2012) it lacked crucial direct proof of *in vivo* aggregation or rearrangements of LHCII antenna triggered by ΔpH and explanation of the role of PsbS protein in the proposed rearrangements (Ruban et al., 2012). To address these important points recently several groups have undertaken a number of approaches (Miloslavina et

al., 2008; Holzwarth et al., 2009; Betterle et al., 2009; Johnson et al., 2011; Ware et al., 2015). Although indirect, however, novel spectroscopic *in vivo* evidence emerged suggesting that upon formation of NPQ a part of the major LHCII complexes undergo separation from the PSII supercomplex and aggregation (Miloslavina et al., 2008; Holzwarth et al., 2009). Further, a biochemical and structural evidence has been obtained suggesting that in NPQ PsbS controlled the dissociation of a part of the PSII–LHCII supercomplex containing LHCII, CP24 and CP29 and that the average distances between PSII core complexes became shorter (Betterle et al., 2009). Later, freeze-fracture electron microscopy studies revealed similar alterations in PSII distances and most importantly clustering of LHCII antenna particles on the protoplasmic fracture face of the stacked thylakoid membrane (PFs) (Johnson et al., 2011; Ruban et al., 2012). This clustering was found to be promoted by the presence of zeaxanthin and PsbS protein (Johnson et al., 2011; Goral, 2012). Further, overexpression of PsbS caused massive LHCII antenna aggregation, even in the absence of RCII complexes (Ware et al., 2015). It was also shown that the antenna composition has a strong effect upon NPQ and the dynamics of the related rearrangements triggered by ΔpH (Goral et al., 2012). Therefore, these advances provided a first direct experimental confirmation of the LHCII antenna aggregation hypothesis of NPQ. Moreover the data showed the common nature of qE and zeaxanthin-dependent qZ NPQ components as manifestations of the same LHCII aggregation phenomenon. Crucially the observed structural alterations induced by illumination occurred on a timescale consistent with the formation and relaxation of qE (Johnson et al., 2011).

Despite all of this progress many details of the *change* that leads to the establishment of the quenched state are not agreed upon or not known at all. Although there is no denial that the LHCII antenna undergoes reorganisation into the NPQ state, recent data suggest that it does not uncouple energetically from RCII (Johnson and Ruban, 2009; Belgio et al., 2014) as was previously proposed (Holzwarth et al., 2009) and in total agreement with the earlier established and experimentally confirmed relationship between the yield of PSII and NPQ (Genty et al., 1989). Moreover it was shown that NPQ protects closed, not open, RCII which makes this protective strategy *economic*, not allowing much competition between NPQ and RCII traps for energy when light intensity is low or moderate (Belgio et al., 2014). Figure 3A depicts a model of the fragment of the grana membrane that shows arrangement of PSII core and LHCII complexes. The arrangement of cores and C2S2M2 supercomplexes (orientation and distances) that contained core dimer, all monomeric LHCII, S and M trimers have been taken from Kouřil et al. (2011). The L trimers were added randomly (positions and orientations) to match the LHCII trimer/RCII ratio of 5. The localisation of PsbS is considered unknown, however the paper of Gerotto et al. (2015) hinted it can be anywhere in the LHCII antenna with a slight preference for the M trimer (Figure

2) although this still needs to be demonstrated for higher plants. In the NPQ state clustering of PSII and LHCII complexes has been displayed schematically adapting the work by Johnson et al. (2011) (Figure 3B). Note that the major assumption here is that the structure of the C2S2 supercomplex is preserved. However, this is not certain (Dong et al., 2015) and has to be verified along with the localisation of PsbS. It was found that this protein changes its conformation (Fan et al., 2015) that can alter, for example, its affinity of binding within the LHCII antenna that could trigger the observed rearrangement. But what is the mechanism of this PsbS effect, its interaction with the LHCII antenna and its specificity? Is the interaction promoted by altered hydrophobicity or potentiated by promotion of N-terminal interactions? If the scheme on the Figure 1B is correct why does PsbS make the LHCII antenna more sensitive to lumen pH? Is it because it somehow enhances hydrophobicity of the environment of proton-receiving aminoacids that can certainly make their pK higher? (Mehler et al., 2002; Thurlkill et al. 2006). Also, while both PsbS and zeaxanthin promote rapid formation of NPQ (Li et al., 2000; Demmig-Adams et al., 1989), why has the former an acceleratory and the latter an inhibitory effect on its recovery as well as opposite effects on chlorophyll excited state relaxation dynamics (Sylak-Glassman et al., 2014)?

Another aspect of the change is LHCII antenna clustering a primary cause of the quenching or is it simply a thermodynamic consequence of the inner conformational change within each trimer or monomer that actually creates the *quencher*? First evidence that isolated LHCII complexes can be quenched without significant aggregation has been obtained by using high hydrostatic pressure or polymerising it into the polyacrylamide gel and gradual removal of detergent (van Oort et al., 2007; Ilioia et al., 2008). The features of this quenching were similar to those of the aggregated low-pH-quenched LHCII. It began to emerge that the LHCII monomer/trimer undergoes some kind of conformational change into the quenching state that involved specific changes in some of the xanthophyll (neoxanthin and lutein) and chlorophyll pigments as was previously observed on LHCII aggregates (Robert et al., 2004; Ilioaia et al., 2011). There exists, however, only the structure of the quenched conformation of trimeric LHCII (Lui et al. 2004; Pascal et al., 2005). Recently a few attempts have been made to understand the scale and possible specificity of the conformational transition into the quenched state. Exciton annihilation experiments along with the high hydrostatic pressure work revealed very small volume alteration of the quenched trimeric LHCII (van Oort et al., 2007; Rutkauskas et al., 2012). NMR studies and accompanying theoretical analysis revealed subtle alterations in some chlorophyll *a* pigments and their interactions with neoxanthin and lutein 1 and 2 (Pandit at al., 2013: Duffy et al., 2014). These observations were consistent with the discovered role of the lumenal loop of trimeric LHCII that is localised close to neoxanthin domain in modulation of quenching *in vitro* (Belgio et al., 2013). This notion was recently confirmed by the first molecular

dynamics study that revealed significant flexibility of trimeric LHCII mostly in neoxanthin and lutein 1 (terminal emitter) domains (Liguori et al., 2015).

In parallel to the structural work on the LHCII antenna, novel single molecule fluorescence spectroscopy of all types of LHCII, trimeric and monomeric, has been intensely applied in recent years (Krüger et al., 2012; 2013; 2014). The rapidly fluctuating levels of the LHCII fluorescence, known as fluorescence intermittency or *blinking*, has been found to be modulated by the xanthophyll cycle composition as well as low pH treatments and therefore closely related to NPQ. The blinking was found to reflect local conformational fluctuations within the complex thermally accessing distinct conformational states that have strong quenching (lutein 1 and 2 domains) or red-shifted fluorescence properties (around 700 nm) (Krüger et al., 2014).

All above mentioned studies on the intrinsic dynamics of the LHCII complexes were absolutely essential in the search of the possible NPQ quencher(s). The quencher is simply 'born' out of the change in conformation triggered by protonation. Currently there are several theories proposing the identity and the physical mechanism of the quenching process. Since this falls out of the scope of this review the reader is referred to the most recent account of the state of the knowledge on the physics of NPQ quencher (Duffy and Ruban, 2015). In brief, pigments zeaxanthin, lutein and chlorophyll *a* have been proposed as possible NPQ quenchers. Zeaxanthin as a quencher was suggested some time ago (Frank et al., 1996; for review see Demmig-Adams, 1990) and recently received strong insightful support from the group of Fleming, Niyogi and Bassi who proposed the quencher localization within the minor LHCII antenna complex CP29 (Holt et al. 2005, Ahn et al., 2008). Lutein bound to the major and minor LHCII as a quencher has also been proposed by several groups (Ruban et al., 2007; Avenson, 2009). Whilst there exist only one theory about the zeaxanthin action as a quenching – a radical cation formation with chlorophyll (Holt et al., 2005), there are several theories explaining how lutein (and other xanthophylls) can quench the excess energy that include coherent and incoherent energy transfer pathways from chlorophyll to xanthophyll (Duffy and Ruban, 2015). Whilst there is some evidence of how zeaxanthin is being activated as a quencher (Holt et al., 2005; Ahn et al., 2008) there is a pool of reports attempting to explain the changes in protein and lutein making this pigment a quencher as well as modelling work assessing the effectiveness of this quencher in taking excess excitation energy from chlorophyll *a* (Ilioaia et al., 2013; Duffy et al., 2013a; 2013b; 2014; Chmeliov et al., 2015). Formation of quenching chlorophyll-chlorophyll dimers has also been recently advocated (Müller et al., 2010). It is worth to note that this multiplicity of the identity and physics of the NPQ quencher(s) may well reflect the complex nature of the process involving formation of a variety pigment-pigment interactions. Therefore the existence of multiple types of quenchers that

include xanthopohylls as well as chlorophylls was recently contemplated (Holzwarth et al., 2009; Liguori et al., 2015).

PROTECTIVE EFFECTIVENESS OF NPQ

The attention to the details of the mechanism of NPQ has been and remains enormous. In contrast, not much is actually known how quantitatively efficient NPQ is in protecting the photosynthetic membrane against photodamage and how to separate its protective component. In addition, there are reports that claim that NPQ plays little or no role in photoprotection of PSII against photodamage (Santabarbara et al., 2001). However, the majority of *in vivo* studies reported observations that clearly established a crucial role of NPQ protection against photoinhibition that led to early senescence and reduction in plant growth and fitness (Niyogi et al., 1998; Verhoeven et al., 2001; Külheim et al., 2002; Niyogi and Truong, 2013). However, a quantitative aspect of protective effectiveness of NPQ and the determination of the critical light intensity plants can tolerate without showing signs of photoinhibition required the development of new approaches. As it was mentioned at the beginning of this review, qE is a rather inaccurate parameter since there are less readily reversible but also protective parts of NPQ different from the qI that reflects photoinhibition. Existing and commonly used measures for photoinhibition include the dark-adapted F_v/F_m ratio or the yield of PSII, O_2 evolution or D1 protein degradation. Whilst these have been effective for assessing the threshold for the damage they have drawbacks for physiological analyses especially where lab-based biochemical analysis is required (D1 turnover). In addition these methods require disruption of the light treatment, either by destructive sampling or imposition of a sustained dark period. The length of the dark period used for F_v/F_m measurements itself can be ambiguous. Recently we developed a novel principle of NPQ analysis that enables a better understanding and quantification of the effectiveness of the protective action of NPQ. In this approach the extent of photochemical quenching (qP) measured in the dark was used to monitor the state of active PSII reaction centres, enabling detection of the early signs of photoinhibition (Ruban and Murchie, 2012; Ruban and Belgio, 2014). It is important to notice that both NPQ/qE and photodamage to RCIIs diminish the quantum yield of PSII. This can be illustrated by the following formula derived by Ruban and Murchie (2012):

$$\Phi_{PSII} = qP \times (F_v/F_m) / [1 + (1 - F_v/F_m) \times NPQ], \quad (1)$$

where qP is the photochemical quenching. F_v/F_m is the yield of PSII before illumination. qP is defined as $(F_m'-F_o'_{act.})/(F_m'-F_o'_{calc.})$, where $F_o'_{act.}$ is a measured dark fluorescence level and $F_o'_{calc.}$ is a dark fluorescence level calculated using Fm' (Oxborough and Baker, 1988). When formula (1) was applied to leaves that had been exposed to gradually increasing light intensity, like in light saturation curves but for longer periods of illumination with short periods of darkness in order to

assess qP levels (Figure 4A), it perfectly matched the experimental data (Figure 4B) up to a certain high actinic light intensity, above which the experimentally determined yield started to decrease more steeply with NPQ than the theoretical value Figure 4B). This discrepancy in the measured and calculated yield came from the fact that qP started to show values lower than 1 (Figure 4B). This is because the measured values of F_o started to become higher than the values of F_o predicted using F_m' amplitude (Oxborough and Baker, 1988) (Figure 4A). This discrepancy comes from the fact that when RCII become closed due to photoinhibition, they stay closed in the dark, hence they cannot photochemically quench fluorescence causing an increase in F_o' in a similar way to the increase in F_o' that would be caused by the addition of DCMU or illumination making this level effectively F_s. Therefore, at this conditions F_o' becomes less appreciably quenched in relation to F_m' that manifests in the observed deviation of the experimental from predicted F_o' levels and hence brings qP level down from 1. This qP was called qP_d to indicate that it was always measured in the dark in the routine of the gradually increasing actinic light intensity (Ruban and Murchie, 2012; Ruban and Belgio, 2014). Critical work has been undertaken to ensure that the novel method is free from artefacts of PSI contribution to the novel PAM fluorescence measurements (Giovagnetti et al., 2015) and that the fluorescence parameter qPd is in good correlation with the electron transport rates measured by oxygen evolution techniques (Giovagnetti and Ruban, 2015).

Application of the described approach enabled the obtaining of a number of important parameters without the need to use the dark relaxation step: a) amplitude of all protective components of NPQ, pNPQ; b) the maximum tolerated light intensity at which all RCIIs remain functional; c) the minimum pNPQ sufficient to protect against the unit of light intensity; d) the amount of potentially wasteful pNPQ: e) the light tolerance curves for a particular type of plant (Ruban and Belgio, 2014; Ware et al., 2014). As a result of this development the highest light intensity tolerated by 50% of various tested plants has been obtained (Figure 4C). One important conclusion of this work is that regardless of the type of mutation, the light tolerance was solely determined by the amplitude of pNPQ (Ruban and Belgio, 2014; Ware et al., 2014). Hence, pNPQ of about 1 in *Arabidopsis* was capable of protecting plants exposed to about 400 μmol $m^{-2}s^{-1}$ PAR. This was an almost linear relationship, meaning that in order to tolerate 1600 μmol $m^{-2}s^{-1}$ PAR of light intensity, almost the highest attainable on the planet (total light intensity of ~3200 μmol $m^{-2}s^{-1}$), plants have to develop pNPQ of about 4, which is probably the top of reported values for this species. As was expected, plants acclimated to low light showed lower light tolerance (Ware et al., 2015). Formation of larger antenna caused higher excitation pressure hence changing the steepness in the relationship between NPQ and tolerated light intensity. Also different plant species differ in their sensitivity to light and therefore the requirement for pNPQ may vary

significantly (Ruban, 2015). In addition, in low light acclimated plants part of the large LHCII antenna was uncoupled from RCII. Interestingly, this uncoupling was associated with increased levels of F_o quenching. However, this additional quenching did not contribute to light tolerance implying that if uncoupled LHCII indeed participated in NPQ process, like was suggested before (Holzwarth et al., 2009) it would contribute little to protection – a fact rendering the existence of two uncoupled sites for NPQ totally unnecessary. In addition, an interesting trend in light tolerance has been observed during ontogenetic development (Carvalho et al., 2015). Seedlings of 1 week old were almost 20 times less tolerant to light than established 8 week old plants. This indicates that the most significant high light damage occurs in young plants or developing leaves. Therefore, the major focus of plant physiologists, ecologists and breeders has to be directed towards monitoring and improving light tolerance specifically at early stages of plant development.

The novel method of NPQ assessment should be very useful in order to evaluate the real effectiveness of NPQ in protection for example in cyanobacteria, diatoms and other classes of photosynthetic organisms. It has got to be realised that the fact of the existence of NPQ is apparently not enough. Modern times require understanding of its value in doing the protective job by analysing in parallel NPQ amplitude and efficiency of photochemistry.

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Figure legends

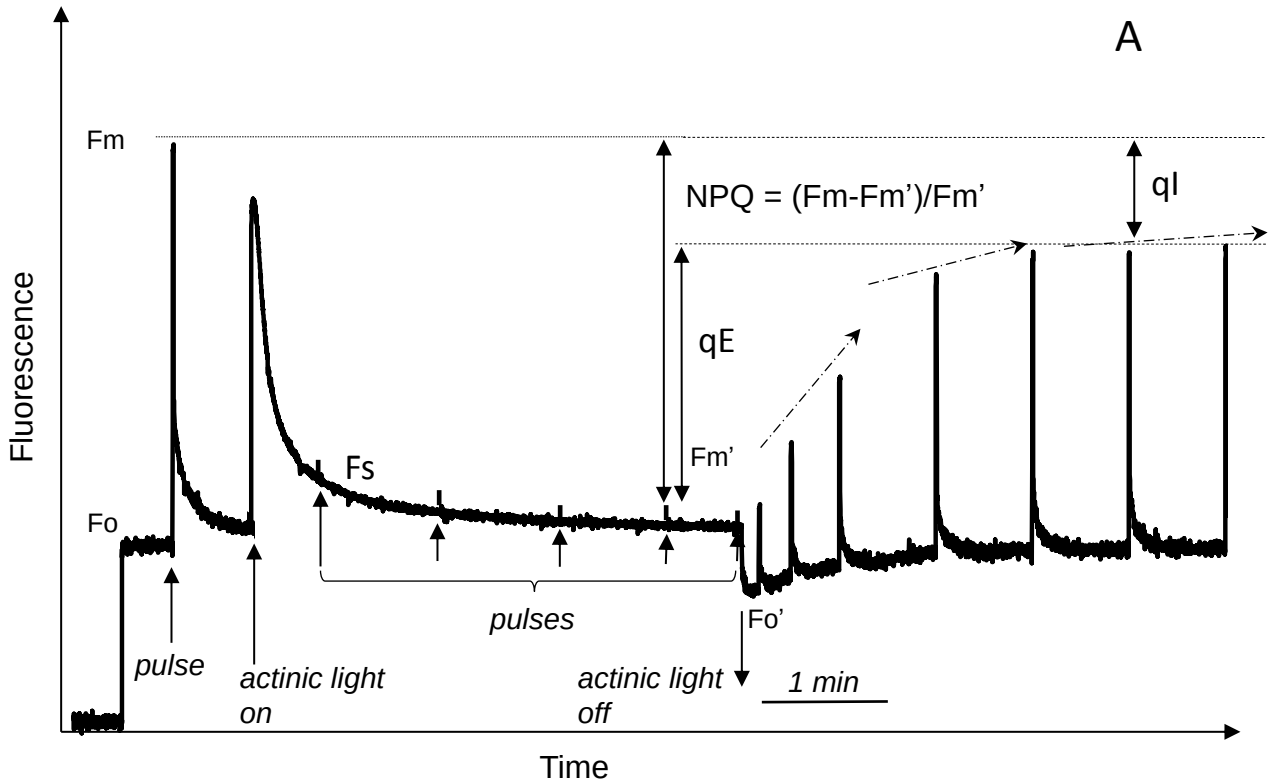
Figure 1. A. Typical PAM fluorescence measurement of Arabidopsis leaf showing induction and relaxation of NPQ. Fm and F_o maximum and minimum fluorescence levels in the dark before actinic light illumination (1000 μmol $m^{-2}s^{-1}$). Fs is a steady state fluorescence level. F_m' is maximum fluorescence during actinic light illumination. Pulses of light (10000 μmol $m^{-2}s^{-1}$) are applied to close all RCII and estimate F_m and F_m'. qE and qI are quickly- and slowly-reversible components of NPQ. **B**. The course of NPQ development, *scenario*, showing key factors triggering and regulating the process (for more details see the text). The formula for the minimum component requirement for NPQ is shown under the diagram.

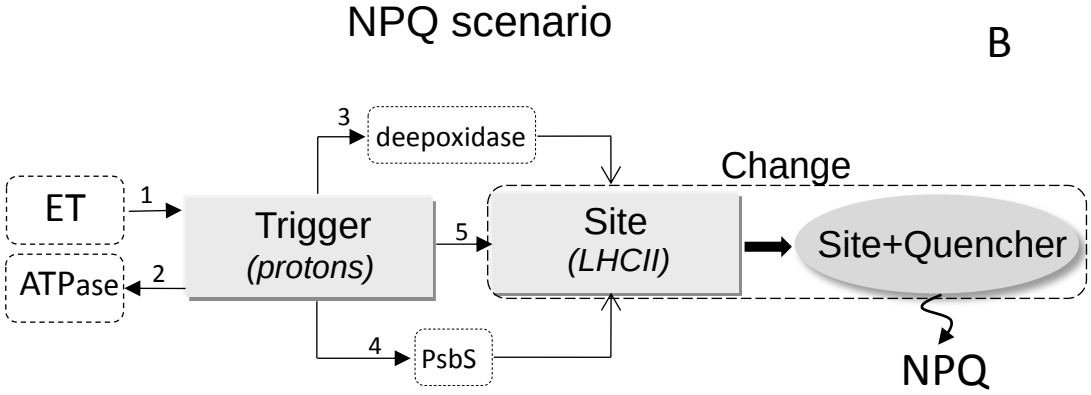
Figure 2. The structure of PSII antenna components. S, M and L are the major LHCII strongly, medium and loosely bound to the RCII core trimers. CP24, 26 and 29 are the minor monomeric antenna complexes. PSII core dimer is shown in red. PsbS dimer is shown with the dashed line pointing to the putative preferential interaction cite in the dark.

Figure 3. The schematic representation of the putative PSII arrangements in the grana membrane in the dark (A) and NPQ (B) states. A. 18 PSII C2S2M2 complexes (outlined by yellow lines) with peripheral LHCII trimers (L trimers) (after Kouřil et al., 2011). Total LHCII trimer to RCII monomer ratio is approx. 5. B. 18 PSII core dimers rearranged/clustered intro the NPQ state (following Johnson et al., 2011). C2S2 structure is shown (outlined with the dashed red line, see the inset) preserved in the 3 supercomplexes shown in the tip left corner. A mix of unquenched (black contour) and quenched (red contour) S, M and L trimers and monomers of the minor antenna (not specified here) is shown. The localisation and interactions of PsbS protein are unknown.

Figure 4. A. A fragment of the gradually increasing illumination procedure in PAM measurement on *Arabidopsis* leaf. The formula on the top shows how qPd was calculated. $F_o'_{act.}$ and $F_o'_{calc.}$ are the measured and calculated (Oxborough and Baker, 1997) dark fluorescence levels. P1, 2, 3 are saturating pulses. AL and FR are actinic and far red light, respectively. 625 and 820 are intensities of actinic light in μmol $m^{-2}s^{-1}$. **B**. The relationships between the PSII yield, qPd and NPQ in the dark in the course of the gradually increasing actinic light intensity procedure (Ruban and Belgio, 2014). The formula shows the relationship between PSII yield, qP and NPQ. **C**. Light intensity (in μmol $m^{-2}s^{-1}$) tolerated by 50% of tested various types of *Arabidopsis* mutant plants: –Zea (npq1); -PsbS (npq4); +PsbS (wt) and ++PsbS (PsbS overexpressor, L17).

Figure 1





NPQ = ΔpH + PsbS + LHCII

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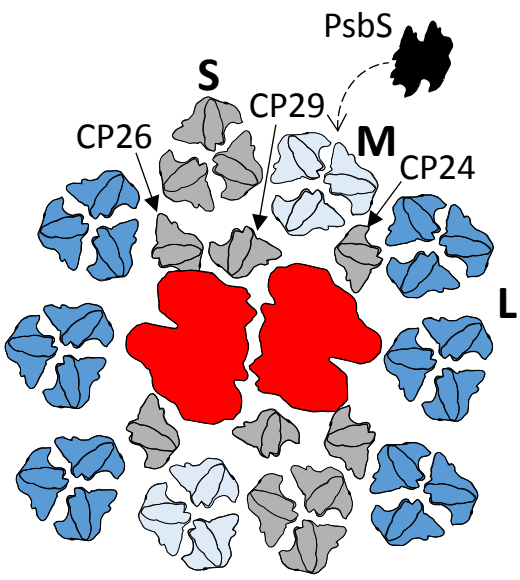

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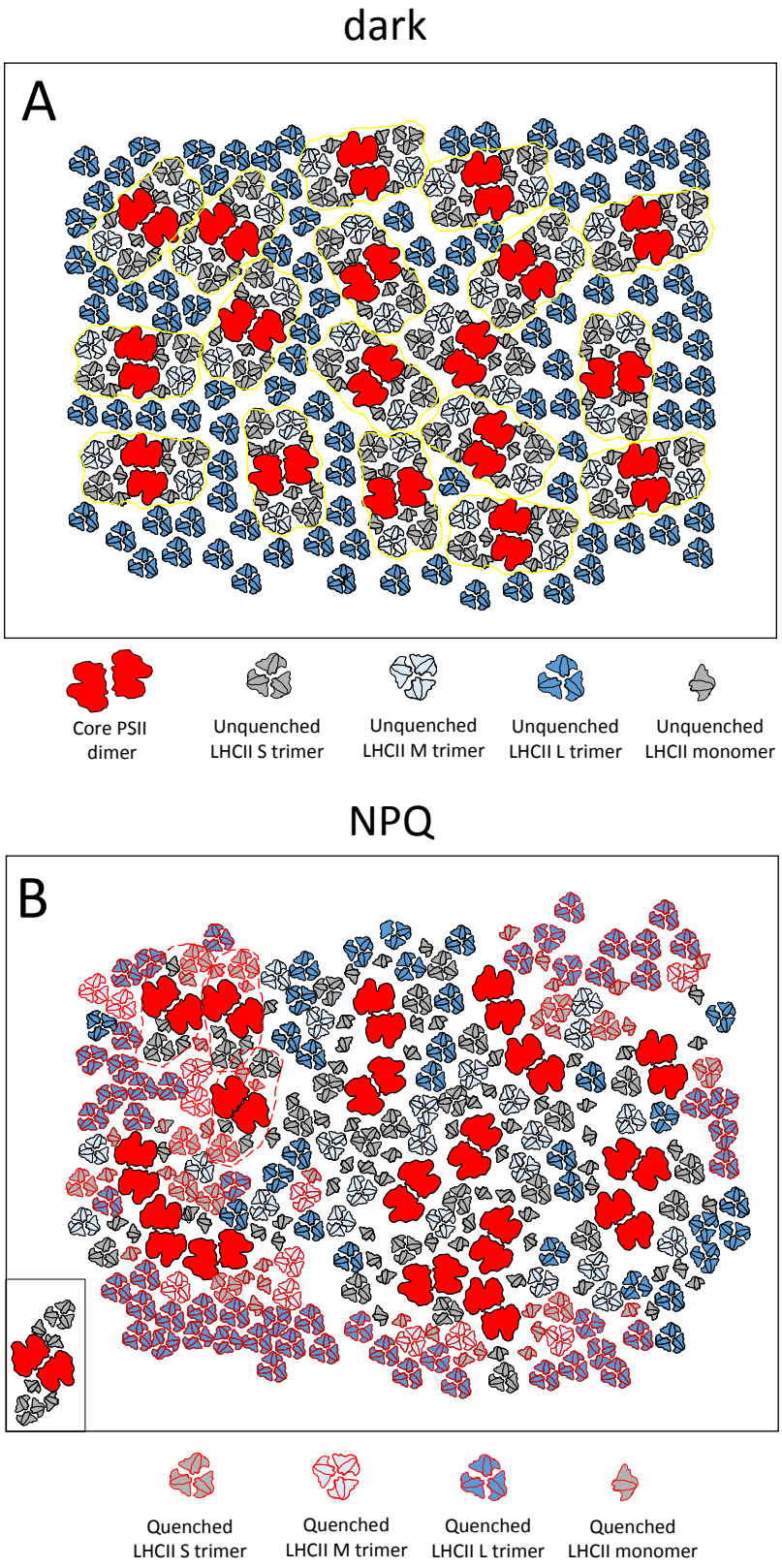

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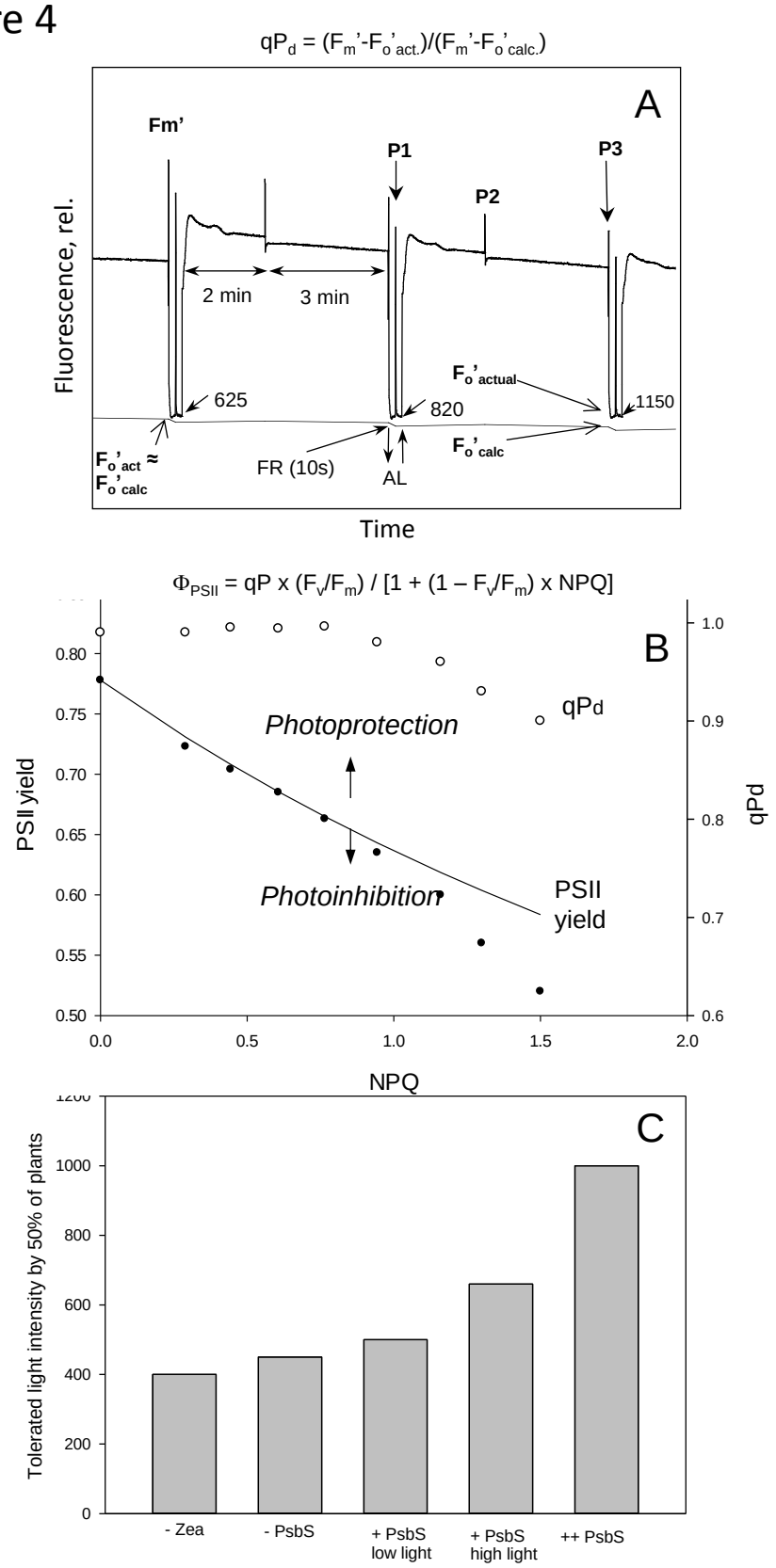

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